



Light-level geolocation reveals wintering distribution, migration routes, and primary stopover locations of an endangered long-distance migratory songbird

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The importance of understanding the geographic distribution of the full annual cycle of migratory birds has been increasingly highlighted over the past several decades. However, the difficulty of tracking small birds between breeding and wintering areas has hindered progress in this area. To learn more about Kirtland's warbler *Setophaga kirtlandii* movement patterns throughout the annual cycle, we deployed archival light-level geolocators across their breeding range in Michigan. We recovered devices from 27 males and analyzed light-level data within a Bayesian framework. We found that most males wintered in the central Bahamas and exhibited a loop migration pattern. In both fall and spring, departure date was the strongest predictor of arrival date, but in spring, stopover duration and migration distance were also important. Though stopover strategies varied, males spent the majority of their spring migration at stopover sites, several of which were located just before or after large ecological barriers. We argue that loop migration is likely a response to seasonal variation in prevailing winds. By documenting a tight link between spring departure and arrival dates, we provide a plausible mechanism for previously documented carry-over effects of winter rainfall on reproductive success in this species. The migratory periods remain the least understood periods for all birds, but by describing Kirtland's warbler migration routes and timing, and identifying locations of stopover sites, we have begun the process of better understanding the dynamics of their full annual cycle. Moreover, we have provided managers with valuable information on which to base future conservation and research priorities.

Understanding the full annual cycle of migratory birds is of fundamental importance (Webster et al. 2002, Harrison et al. 2011, Small-Lorenz et al. 2013, Marra et al. 2015), in part because populations can be limited during any part of their annual cycle (i.e. breeding, wintering, migration; Sherry and Holmes 1995, Newton 2004, 2006, Runge and Marra 2005, Drake et al. 2014). Understanding the full annual cycle requires knowing where and when individuals and populations are located throughout the year. Up until the past decade, tracking small migratory birds as they travel from their breeding grounds often thousands of kilometers along a network of resting and re-fueling (i.e. stopover) sites to their wintering grounds was impossible. However, miniaturization of tracking technologies has recently allowed researchers to track smaller birds for longer periods of time than ever before (Bridge et al. 2013, Hallworth and Marra 2015). Moreover, new analytical tools allow for increasingly accurate estimates of location (Rakhimberdiev et al. 2016) and quantification of error (Sumner et al. 2009). While the use of such tools has rapidly increased our ability to identify wintering areas, information regarding migratory routes, stopover sites, and migratory connectivity (i.e. how breeding, migratory, and wintering populations are

geographically linked; Webster et al. 2002) is still lacking for most species.

However difficult, the importance of understanding the full annual cycle of birds is clear. For example, in migratory songbirds it appears that a significant amount of mortality occurs during migration itself (Sillert and Holmes 2002, Rockwell et al. 2016), suggesting that factors en route are critical to population dynamics (Drake et al. 2014). However, events prior to migration can influence performance both during migration and in subsequent periods. As an example of such carry-over effects, poor quality winter habitat has been shown to delay both departure on spring migration (Marra et al. 1998, Studds and Marra 2005, Cooper et al. 2015), and arrival on the breeding grounds (Tonra et al. 2011, Rockwell et al. 2012, Paxton and Moore 2015, but see McKinnon et al. 2015), which in turn negatively affects reproductive success (Cooper et al. 2011, McKellar et al. 2013). Carry-over effects can also influence survival. For example, precipitation on the wintering grounds drives variation in food availability (Strong and Sherry 2000, Williams and Middleton 2008), and has been shown to predict annual survival and/or breeding abundance in several species (Baillie and Peach 1992, Szép 1995, Wilson et al.

2011). Clearly, understanding each phase of the annual cycle and how events in one period interact with subsequent periods is of critical importance, particularly for threatened and endangered species.

The Kirtland's warbler *Setophaga kirtlandii* is a Nearctic-Neotropical migratory songbird that breeds almost exclusively in Michigan, USA (Bocetti et al. 2014). They are known to winter throughout the Bahamian Archipelago (Bocetti et al. 2014), but it is not well understood how the population is distributed across their wintering range. The U.S. Fish and Wildlife Service declared the species endangered in 1966, though creation of breeding habitat and control of brown-headed cowbird *Molothrus ater* populations on the breeding grounds has led to substantial recovery of the population. Despite these management successes, Kirtland's warblers, like all migratory birds, face a multitude of threats outside of the breeding period including climate-change and human-induced habitat loss (Wunderle et al. 2010, 2014, Rockwell et al. 2012). The importance of a full annual cycle perspective is further highlighted by the finding that March rainfall in The Bahamas influences Kirtland's Warbler migration timing, reproductive success, and annual survival, with ~ 44% of annual mortality occurring during migration (Rockwell et al. 2012, 2016). While conditions on the wintering grounds are clearly important determinants of reproductive success and survival, factors during migration itself are almost certainly important as well, but remain unstudied.

Without knowledge regarding how birds are distributed across their wintering range, when and where migration occurs, and what factors drive individual differences in the timing of migration, understanding the full annual cycle and taking appropriate conservation actions is not possible. To provide managers with new information on which to base conservation and research priorities, we used light-level geolocators to: 1) describe the wintering distribution of Kirtland's warblers, 2) identify fall and spring migration routes, 3) explore how factors such as departure date, migration distance, and wintering location influence the duration and timing of migration, and 4) locate important stopover areas used during migration.

Methods

In 2012 and 2014, we captured adult male Kirtland's warblers using mist nets, and banded each bird with one U.S. Geological Survey band and three colored plastic bands. We sexed and aged birds (Pyle 1997), measured their mass with a digital scale (0.01 g) and took standard morphological measurements. In 2012, we attached 0.65 g archival light-level geolocators (hereafter geolocators; Lotek MK6740) to 24 after-second year (ASY) males. In 2014, we attached 0.55 g geolocators (Lotek ML6740) to 60 ASY males. In both years, we used the leg-loop method (Rappole and Tipton 1991) to attach geolocators. Geocator mass plus attachment materials varied from 4.0 to 5.1% of body mass ($\bar{x} \pm SD = 4.5 \pm 0.32\%$). All geolocators had 15 mm stalks positioned at a 30° angle to the body of the device.

In 2012, all geolocators were deployed in the center of the breeding range, but in 2014 we deployed geolocators

across the entire north-south expanse of the breeding range in the Lower Peninsula of Michigan (44.15°N to 45.25°N). Males that did not receive geolocators (2012: $n = 29$, 2014: $n = 32$), served as controls so that we could compare return rates the following year. However, due to limited personnel, minimal effort was put into re-sighting in 2013, and therefore we could not test for differences in return rate in that year.

Light-level analysis

Light-level geolocation involves the estimation of sunrise and sunset times to determine geographic location based on known variation in day length and solar noon across the globe (Hill and Braun 2001). We refer to sunrise and sunset times throughout, but these actually refer to the times during the twilight periods (i.e. dawn to sunrise and/or sunset to dusk) when the sun is at a user-defined angle (i.e. sun elevation or zenith angle; see Supplementary material Appendix 1 for more details). We used package 'GeoLight' (Lisovski and Hahn 2012) to estimate sunrise and sunset times using the threshold method (Hill and Braun 2001). We then analyzed light-level data within a Bayesian framework using the Solar/Satellite Geolocation for Animal Tracking (SGAT) package (Wotherspoon et al. 2013) for program R (R Core Team). SGAT uses Markov Chain Monte Carlo (MCMC) simulations to estimate location and quantify the error inherent in light-level geolocation. We provided SGAT with: 1) raw position estimates derived using the threshold method, 2) a model describing error in sunrise and sunset determination, 3) a behavioral model defining probable flight speeds, and 4) a spatial probability mask that made locations over water less likely, but not impossible. Using three independent chains, we drew 120 000 samples for burn-in and tuning, and a final 15 000 samples to define the posterior distribution, where each sample represented one set of estimated locations. Estimation of latitude surrounding the equinoxes is inaccurate because of low variation in day length (Lisovski et al. 2012). However, we used the behavioral model and spatial probability mask to discard unrealistic latitudinal estimates near the equinoxes. Nonetheless, some uncertainty in these estimates still exists.

Using position estimates drawn from posterior distribution, we defined the breeding and wintering ranges as the 95th quantiles of positions during periods of known occupancy in Michigan (deployment date until 25 July) and on the wintering grounds (15 November–27 February). To estimate each male's movement path throughout the year, we calculated the mean path from all 15 000 samples. Fall and spring departure dates were defined as the first days the paths exited, without returning, the breeding and wintering grounds respectively. Likewise, fall and spring arrival dates were defined as the first days the paths entered, without exiting, the wintering and breeding grounds respectively. For each male, we estimated spring migration distance by determining the shortest great circle distance between successive points along each bird's path, assuming that males were stationary at the centroid of each stopover area for the duration of each stopover period. Fall migration distance was not estimated because stopover periods could not be determined due to the autumnal equinox (see below).

We used functions within package ‘GeoLight’ to determine stationary and movement periods during migration. For spring migration, this allowed us to quantify the time spent at, and general location of, stopover sites. Due to uncertainty in latitudinal estimation near the equinoxes, we were unable to use this method to identify stopover locations during fall migration. Instead, we identified fall stopover locations using time-spent maps produced in SGAT. Time-spent maps indicate the probability of residency relative to the period of inquiry. For migratory periods, a time-spent map depicts the probability of residency relative to the duration of the migration period. Locations of higher probability indicate that individuals spent more time at a particular location relative to the other locations, and therefore indicate likely stopover areas. During stationary periods (i.e. breeding/wintering) the time-spent map illustrates the probability of occurrence at that location for the duration of the period. To investigate the fall stopover period for each male, we created a time-spent map of the fall migration period. We then combined the 95th quantiles of positions during fall migration for all males into a single raster to identify stopover areas. For full light-level analysis details, see Supplementary material Appendix 1. All light-level data and example R code are available on Movebank (<www.movebank.org>, ‘Kirtland’s warbler Michigan’).

Statistical analysis

To test for differences in apparent survival between control males and males with geolocators we used a chi-squared test. To better understand how breeding and wintering location, migration distance, and departure date were related to arrival date, we used Pearson’s correlations and Pearson’s partial correlations. We then entered spring departure date, total time on stopover, and migration distance as independent variables into a linear regression with spring arrival date as the dependent variable. To compare fall and spring migration directly, we used Pearson’s correlations to determine if fall and spring arrival dates were correlated and whether fall and spring departure dates were correlated. Finally, we compared the duration of spring and fall migration using a t-test. All statistical tests were carried out in PASW 18.0 (IBM, Armonk, New York, USA). All means are reported ± 1 SE unless otherwise noted.

Data available from Movebank Data Repository: doi: 10.5441/001/1.h2b30454 (Cooper et al. 2016).

Results

We recovered 6 of 24 (25%) geolocators deployed in 2012, and 24 of 60 (40%) geolocators deployed in 2014. Each year, one male returned without a geocator, and in 2014 three devices failed to record usable data. The remaining 27 devices all successfully recorded data from deployment until recovery ($\bar{x} = 351 \pm 3.1$ d). In 2015, we re-sighted 18 of 32 (56%) control males and 28 of 60 (47%) males with geolocators. This difference in return rate was not significant ($\chi^2 = 0.77$, DF = 1, $p = 0.381$). Our estimate of return rate for males with geolocators is within the range of adult survival for this species (0.58 ± 0.11 ; Rockwell

et al. 2016). Moreover, the median spring arrival date of males with geolocators (12 May) was nearly identical to the median spring arrival date of 220 color-banded males (13 May), whose arrival dates were estimated via direct observation at the same sites in Michigan (Rockwell et al. 2012). Our mean spring migration duration (15.7 ± 0.75 d) was also nearly identical to that of five males (15.8 ± 4.2 d) banded on the wintering grounds and later re-sighted on the breeding grounds (Ewert et al. 2012). Thus, our data strongly suggest that males were not negatively affected by carrying geolocators and exhibited typical migration behavior (reviewed by Costantini and Møller 2013).

All tracked males wintered in the Caribbean, spending 185 ± 1.4 d on the wintering grounds. The estimated wintering ranges of 18 males (67%) overlapped primarily the central Bahamas (i.e. Eleuthera, Cat Island, The Exumas, Long Island, Rum Cay, San Salvador), four males (15%) overlapped primarily the western Bahamas (i.e. Grand Bahama, The Abacos, Nassau, Andros Island), and four males (15%) overlapped primarily the eastern Bahamas (i.e. Acklins Islands, Mayaguana, Great Inagua) or Turks and Caicos (Fig. 1). One male (4%) appeared to winter in central Cuba, but because the northern edge of his estimated wintering range overlapped South Andros in The Bahamas, we cannot entirely rule out South Andros out as his wintering location. Eastern Cuba and northernwestern Haiti were overlapped slightly by a few other estimated winter ranges, but only at the edges, indicating low probability of residency. As no sighting data from eastern Cuba or Haiti exist, we regard these areas as unlikely wintering locations.

All but five males showed a loop migration pattern, with an easterly route in the fall and a westerly route in the spring (e.g. Fig. 2). Of the five males that did not exhibit a loop migration, three used the easterly fall migration route, but during both fall and spring migration. These three males departed the wintering grounds (25, 26, 28 April) around the same time as all other males ($\bar{x} = 27$ April ± 1.53 d) and

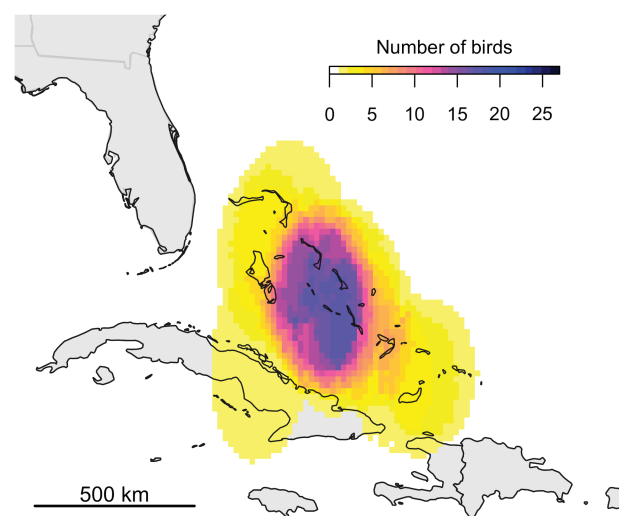


Figure 1. Winter distribution of 27 male Kirtland’s warblers *Setophaga kirtlandii*. Map was created by combining the 95th quantiles of all males’ positions from 15 November to 27 February into a single raster. Colors indicate the number of birds overlapping in space.

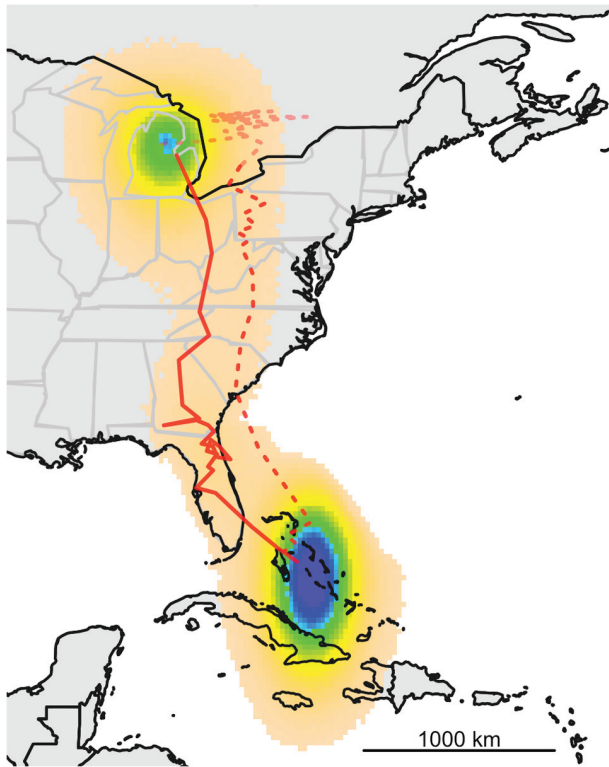


Figure 2. Relative probability of residency of one male Kirtland's warbler *Setophaga kirtlandii* for one year. Probability of residency increases from peach to blue indicating that this male spent most of the year on the wintering grounds. The outer bounds of the colored area represent the lowest probability positions. The means of the posterior distribution are shown for fall (dashed red line) and spring migration (solid red line).

arrived to the breeding grounds (12, 14, 24 May) around the same time as all other males ($\bar{x} = 13 \text{ May} \pm 4.5 \text{ d}$). The other two males that did not perform a loop migration instead flew straight south from the breeding grounds, left the Florida coast towards the wintering grounds, and used a similar route in the spring. These two males arrived somewhat late on the wintering grounds (1 and 8 November) compared to all other males ($\bar{x} = 24 \text{ October} \pm 5.2 \text{ d}$).

Timing of migration

Males departed the breeding grounds on fall migration over a one-month period in September and October (Table 1), arriving to the wintering grounds $18.1 \pm 1.53 \text{ d}$ later. The fall migratory period of five males completely overlapped the autumnal equinox period. Furthermore, two males' first detectable migratory movements were southwards. Because of the uncertainty of latitudinal estimates near

the autumnal equinox, we could not accurately determine departure date for these seven individuals. For the remaining males, fall departure and arrival dates were not correlated with either breeding or wintering locations. However, males that departed on fall migration early arrived to the wintering grounds early (Fig. 3a). Also, males that departed late from the breeding grounds had shorter migration durations, indicated by the negative correlation between fall departure date and migration duration (Table 2).

Males initiated spring migration in late April and early May, and arrived on the breeding grounds $15.7 \pm 0.75 \text{ d}$ later (Table 1). Spring migration distance ranged from 2340 to 3512 km ($\bar{x} = 2811 \pm 46.4 \text{ km}$) depending on wintering location. Spring departure date did not correlate with wintering location, breeding location, or migration distance. Winter latitude had no effect on spring arrival date, but males that wintered in the western part of the range arrived earlier than those in the east (Table 2). This was likely due to the fact that males departing from the western islands of the wintering range had shorter migration distances ($r = 0.704$, $n = 27$, $p \leq 0.001$), and shorter migration durations (Table 2). Correspondingly, after controlling for migration distance, the relationship between arrival date and winter longitude was no longer significant ($r_p = 0.372$, $DF = 24$, $p = 0.062$). Just as in the fall, males that departed early from the wintering grounds also arrived early on the breeding grounds (Table 2, Fig. 3b). Together, spring departure date ($\beta = 0.99$, $t = 11.94$, $p \leq 0.001$), total time spent on stopover ($\beta = 0.829$, $t = 9.92$, $p \leq 0.001$), and migration distance ($\beta = 0.01$, $t = 4.74$, $p \leq 0.001$), explained nearly all of the variation in spring arrival date ($F = 86.98$, $DF = 26$, $p \leq 0.001$, $R^2 = 0.908$).

Comparing fall and spring migration

To compare fall and spring migration we looked for relationships between fall and spring departure date, arrival date, and migration duration. Fall departure date from the breeding grounds was not correlated with spring departure date from the wintering grounds ($r = -0.068$, $n = 22$, $p = 0.777$). Similarly, fall and spring arrival dates were not correlated ($r = -0.015$, $n = 20$, $p = 0.946$). Fall and spring migration durations were also not correlated ($r = -0.099$, $n = 20$, $p = 0.677$). Fall migration ($18.1 \pm 1.53 \text{ d}$) was slightly longer in duration than spring migration ($15.7 \pm 0.75 \text{ d}$) but the difference was not significant ($t = 1.54$, $DF = 29.6$, $p = 0.134$).

Stopover locations

We identified three primary stopover regions used by much of the population during fall migration. After departing the

Table 1. Kirtland's warbler *Setophaga kirtlandii* departure, jump off, landfall, and arrival dates during fall and spring migration. Jump off date is the first day each bird began over-ocean flight during fall migration, and landfall date is the first date each bird crossed onto the continental United States during spring migration. Date ranges are shown with $\bar{x} \pm 1 \text{ SE}$ in parentheses.

	Fall migration	Spring migration
Departure date	24 Sep.–24 Oct. (6 Oct. ± 1.7)	22 Apr.–5 May (27 Apr. ± 0.7)
Jump off/landfall date	15 Oct.–27 Oct. (21 Oct. ± 1.0)	24 Apr.–9 May (30 Apr. ± 0.8)
Arrival date	18 Oct.–8 Nov. (25 Oct. ± 1.3)	5 May–25 May (13 May ± 0.9)

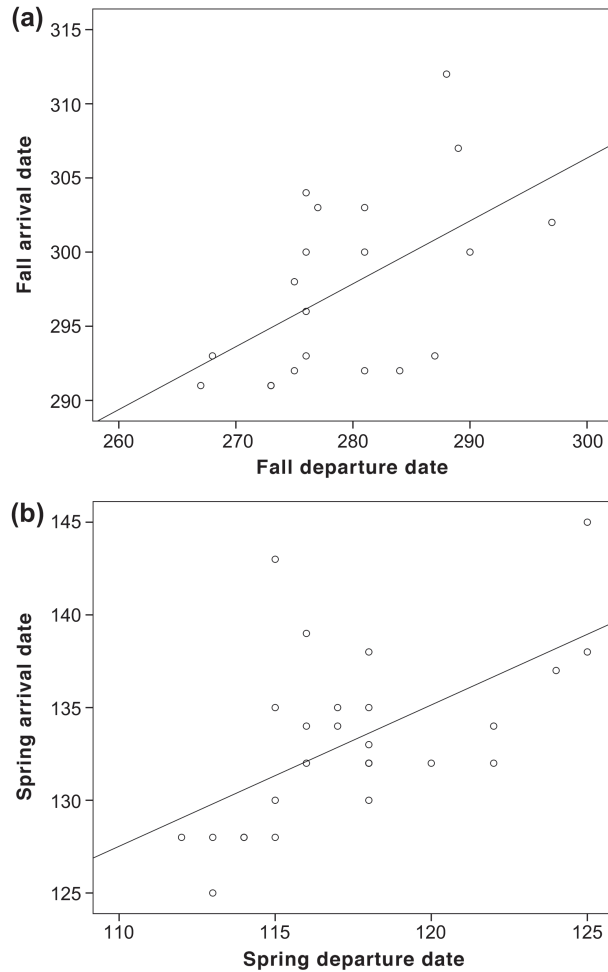


Figure 3. Relationships between departure and arrival dates (day 1 = 1 January) for fall (a) and spring (b) migrations of male Kirtland's warblers *Setophaga kirtlandii*.

breeding grounds in an eastward direction, 25 of 27 males stopped over in southern Ontario or the northwestern Mid-Atlantic States (Fig. 4a). Most males initiated open-water migration after stopping over on the coastline of either North or South Carolina, but two males did so from Florida (Fig. 5a). Near the end of fall migration, those males that wintered in the eastern Bahamian Archipelago first stopped over in the western Bahamas (Fig. 4a).

During spring migration, males made between one and five stopovers ($\bar{x} = 2.4 \pm 0.16$ stopovers), spending the majority ($58 \pm 2.4\%$) of their spring migration at stopover sites. While stopover strategies varied, we identified three stopover areas used by much of the population during spring

migration. First, most males (20/27; 74%) made a stopover (\bar{x} duration = 4.8 ± 0.80 d) shortly after making landfall in Florida (Fig. 5b), while the remaining seven (26%) travelled further north before making their first stopover. Second, somewhere in northern Florida, southeastern Georgia, or southwestern South Carolina, 26 of 27 (96%) males spent between 1.5 and 14.5 d ($\bar{x} = 4.7 \pm 0.67$ d) before crossing the Appalachians (Fig. 4b). Southwestern Ontario and the region directly to the south also appeared to be important, with nine males (33%) spending between 1 and 3.5 d ($\bar{x} = 2.2 \pm 0.26$ d) there before reaching Michigan. See Supplementary material Appendix 1, movie for an animation of the full annual cycle (2014–2015).

Discussion

Our tracking data confirmed that Kirtland's warblers winter almost exclusively in the Bahamian Archipelago, with the majority of birds wintering in the central Bahamas. We documented loop migration in nearly all males, and described the timing of both fall and spring migration. We found that departure date was the strongest predictor of arrival date for both fall and spring migration. We narrowed down the location of stopover sites to broad regions for both migratory periods for the first time. Below, we discuss each of these findings and their conservation implications in detail.

Wintering distribution and migration patterns

The Kirtland's warbler wintering range was thought to be restricted to the Bahamian Archipelago (Bocetti et al. 2014) and our data generally match these observations, with the majority of tracked males wintering in the central Bahamas. However, we did find that one male wintered in central Cuba. Two previous sightings from Cuba exist, both on the northern island of Cayo Coca (Isada 2006, S. Musgrave pers. comm.). The probable wintering range of the male we tracked to Cuba overlaps this island, but also includes a large portion of mainland Cuba (Fig. 1). Assuming that our sample is representative, our data suggest that the majority (~66%) of Kirtland's warblers winter in the central Bahamas with the remaining birds wintering primarily in the eastern and western Bahamas, and a small number wintering in Cuba. These results are supported by ~15 yr of unpublished survey data (D. N. Ewert and J. M. Wunderle pers. comm.), which show the highest abundance in the central Bahamas and lower abundance in the eastern and western Bahamas and Turks and Caicos.

Table 2. Pearson's correlations between departure date, arrival date, breeding location, wintering location, and migration duration for male Kirtland's warblers *Setophaga kirtlandii*. Significant correlations are bolded.

	Fall departure	Fall arrival	Spring departure	Spring arrival
Breeding latitude	$r = 0.28$, $p = 0.236$	$r = -0.09$, $p = 0.683$	$r = -0.07$, $p = 0.725$	$r = -0.01$, $p = 0.980$
Breeding longitude	$r = 0.32$, $p = 0.171$	$r = -0.17$, $p = 0.453$	$r = 0.236$, $p = 0.236$	$r = 0.17$, $p = 0.393$
Winter latitude	$r = 0.23$, $p = 0.896$	$r = -0.03$, $p = 0.902$	$r = 0.054$, $p = 0.787$	$r = -0.062$, $p = 0.419$
Winter longitude	$r = 0.03$, $p = 0.341$	$r = 0.10$, $p = 0.664$	$r = -0.062$, $p = 0.759$	$r = 0.394$, $p = 0.042$
Migration duration	$r = -0.65$, $p = 0.002$	$r = 0.30$, $p = 0.195$	$r = -0.22$, $p = 0.278$	$r = 0.67$, $p \leq 0.001$
Arrival date	$r = 0.53$, $p = 0.016$			$r = 0.58$, $p = 0.002$

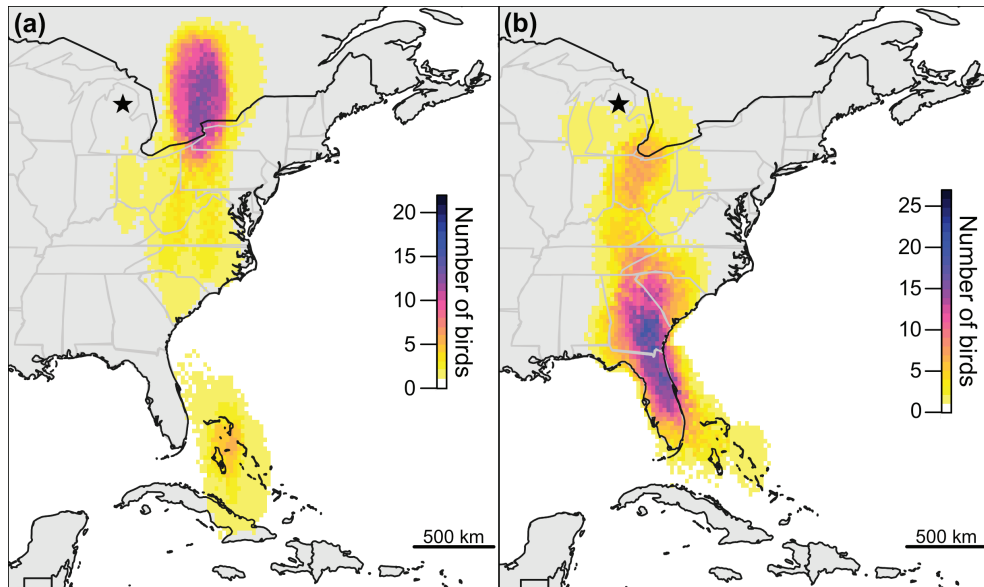


Figure 4. Fall (a) and spring (b) stopover locations for migrating male Kirtland's warblers *Setophaga kirtlandii*. Fall map was created by taking the 95th quantiles of positions estimated during each male's fall migration period and combining them into a single raster. Spring map was created by taking the 95th quantile of positions estimated during each male's spring stopover periods and then combining them into a single raster. Colors indicate the number of birds overlapping in space and the star indicates the Michigan breeding grounds.

Similar to many other species (La Sorte et al. 2013, McKinnon et al. 2013), we found that most Kirtland's warblers exhibited a loop migration pattern. Loop migration was predicted in Kirtland's warblers by a least-cost model that incorporated elevation and wind (Winters 2015). Moreover, Gauthreaux et al. (2005) analyzed long-term wind data and showed that in September and October prevailing winds were favorable for southward migration along

the mid-Atlantic route taken by all but two of our males (see also La Sorte et al. 2014a, Kranstauber et al. 2015). Thus, it is possible that loop migration in Kirtland's warblers is a response to geographic variation in prevailing wind patterns. However, La Sorte et al. (2014b) showed that ecological productivity likely also drives loop migrations, though the relationships they found were stronger in the western flyway than in the eastern flyway used by Kirtland's warblers. It

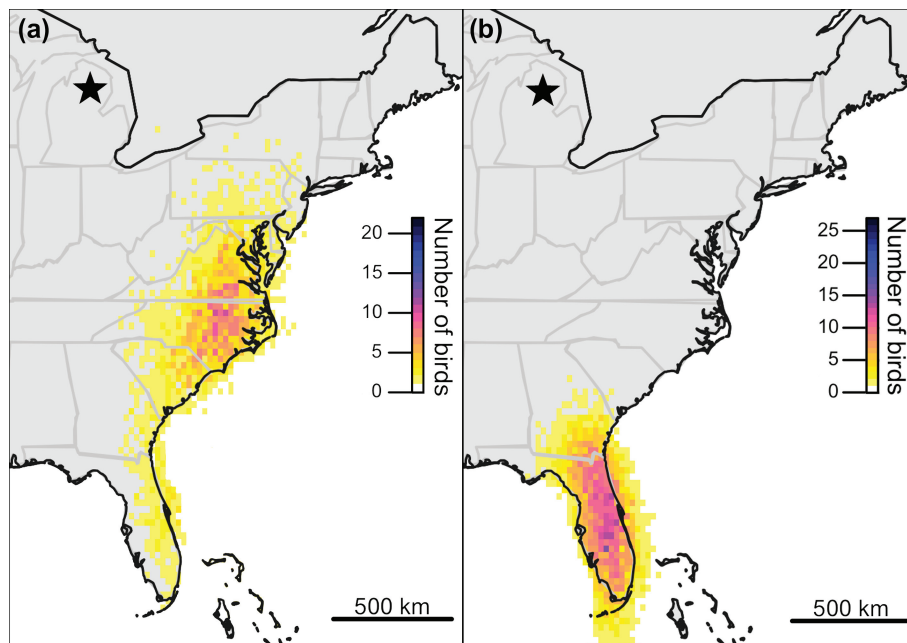


Figure 5. Map indicating where each male Kirtland's warbler *Setophaga kirtlandii* first began over-ocean flight during fall migration (a) and first made landfall on the continental United States during spring migration (b). In both cases, maps were created by taking the 95th quantiles of positions from the appropriate day and combining them into a single raster. Colors represent the number of birds overlapping in space and the star represents the Michigan breeding grounds.

remains unclear why two males migrated straight south from the breeding grounds and did not use the easterly fall route that the rest of the population used, but these males were among the last to depart on fall migration. It is possible that prevailing winds had changed by the time they departed, and that they modified their routes accordingly. However, further research is needed to determine how migratory movements of small passerine birds match spatiotemporal variation in atmospheric and ecological conditions.

Migration timing

In contrast to other studies, fall and spring migration were similar in duration (reviewed by McKinnon et al. 2013). This suggests that for Kirtland's warblers, early arrival on the wintering grounds is as important as early arrival on the breeding grounds (Newton 2008, Tøttrup et al. 2012). However, we did not find correlations between fall and spring departure dates or fall and spring arrival dates, which indicates that in contrast to red-eyed vireos *Vireo olivaceus* (Callo et al. 2013), male Kirtland's warblers that depart and arrive early on fall migration do not also depart and arrive early on spring migration. This, in turn, suggests that habitat quality, weather, or other environmental factors are likely more important in determining migration timing than some fixed aspect of male quality (e.g. age, body size, wing length).

Patterns of departure from the breeding grounds have not been explored in Kirtland's warblers, or most other species (but see Vega Rivera et al. 1998, Mills 2005, Stutchbury et al. 2010). Kirtland's warblers undergo a complete molt from mid-August to late September (Sykes et al. 1989). We found that most males in our study departed the breeding grounds in an eastward direction in September or October, presumably shortly after finishing their prebasic molt. Mills (2005) suggested that selective pressure for males to remain on breeding territories late into autumn might exist because of benefits associated with territory acquisition or re-acquisition the following spring. Regardless, habitat use by Kirtland's warblers, and most other species, is poorly understood during this period, but is probably important given the energetic demands of molt (Cyr et al. 2008) and the risk of mortality resulting from temporary reduction in flight ability (Swaddle and Witter 1997).

Similar to fall departure, little is known about patterns of arrival on the wintering grounds (but see Marra 2000). Males in our study arrived to the wintering grounds in late October and early November, and we found that the only significant predictor of fall arrival date was the date each male departed from the breeding grounds. Each 3-d delay in fall departure delayed arrival on the wintering grounds by ~ 1.2 d. However, males that departed late on fall migration had shorter migration durations, suggesting two possible pathways to early arrival on the wintering grounds; early departure and shorter migration duration. The fact that late departing males spent less time on migration than early departing males suggests selection pressure to arrive early on the wintering grounds (Newton 2008, Tøttrup et al. 2012). Most Kirtland's warblers do not hold season-long winter territories, instead holding territories for shorter periods of time. Nonetheless, competition over food resources, as

evidenced by age- and sex-based competitive interactions, clearly exists (Wunderle et al. 2014). Thus, gaining priority access to wintering sites through early arrival may be both possible and advantageous.

In contrast to fall, patterns of spring migration timing and their consequences are better understood. March rainfall explains much of the between-year variation in spring arrival date in young male Kirtland's warblers (Rockwell et al. 2012), but this study did not reveal the drivers of individual, within-year variation. We found that spring arrival date was best predicted by spring departure date (see also McKinnon et al. 2013). Establishing a tight link between spring departure and arrival dates provides a mechanism by which the previously established carry-over effects of winter rainfall on reproduction in Kirtland's warblers can occur (Rockwell et al. 2012). However, spring departure was not the only determinant of spring arrival; total time spent at stopover sites (see also McKinnon et al. 2016) and migration distance were also important. For each additional day a male spent on the wintering grounds, 1.2 extra days spent on stopover, or additional 167 km traveled, their arrival on the breeding grounds was delayed by one day, suggesting three independent pathways to early arrival.

Regardless of the pathway, early spring arrival is an important determinant of reproductive success in Kirtland's warblers (Rockwell et al. 2012) and many other species (see Introduction). Across the range of arrival dates in our study, the earliest arriving males would likely fledge 1.5 more young than the latest arrivers (Rockwell et al. 2012), which represents a substantial difference in reproductive success given that Kirtland's warblers are single-brooded and typically lay 4–5 eggs (Bocetti et al. 2014). Thus, discovering the factors that influence spring departure date, stopover duration, and wintering location is crucial if we are to understand the mechanisms by which conditions on the wintering grounds and conditions during spring migration interact to influence breeding season dynamics.

The beginning of migration is ultimately controlled by changes in photoperiod (Dawson et al. 2001), but evidence from other species indicates that departure date can be modified by food availability and body condition (Studds and Marra 2005, 2007, 2011, Fox and Walsh 2012). For example, Cooper et al. (2015) demonstrated that experimentally reduced food availability and the resulting poor body condition, led to about a one-week delay in spring departure date in American redstarts *Setophaga ruticilla*. For Kirtland's warblers, a one-week delay in departure would lead to about a one-week delay in arrival on the breeding grounds. However, it appears that late departing Kirtland's warblers can partially compensate for late departure by spending less time on stopover (see also McKinnon et al. 2015) or possibly wintering closer to the breeding grounds. In other species, factors such as body condition (Fusani et al. 2009), fat deposition rates (Goymann et al. 2010), weather (Dossman et al. 2016), predation (Alerstam 2011), and the density of conspecifics (Shochat et al. 2002) all influence stopover duration. These factors are likely important in determining stopover duration of Kirtland's warblers, but further investigation is needed. It is unclear whether Kirtland's warblers might modify their wintering location at a large enough scale (i.e. between rather than within islands) to be able to improve arrival timing on

the breeding grounds. Regardless, the importance of early arrival to reproductive success in this species suggests that wintering closer to the breeding grounds results in fitness gains.

Stopover locations

Given the energetic demands of long-distance flight and the high-risk of mortality during migration (Sillett and Holmes 2002, Rockwell et al. 2016), resting and re-fueling in high-quality habitat along the migration route is important for a successful migration (reviewed by Alerstam 2011). Similar to other species, Kirtland's warblers spent the majority of the migratory period at stopover sites, with some males spending a week or more at individual stopover sites. Such long stopovers are not uncommon (6 of 18 species reviewed by McKinnon et al. 2013), but the fact that males spent so much time on stopover and that many of the stopover areas were located just before or after ecological barriers, highlight the importance of determining their location. Due to technological limitations in light-level geolocation, we could not identify the exact location of stopover sites. However, we were able to narrow down the location of stopover sites to broad regions for the first time in this species.

During fall migration, nearly all males first stopped somewhere in southeastern Ontario or the northwestern Mid-Atlantic states after departing the breeding grounds in Michigan. The latitudinal estimates during the first part of fall migration should be interpreted with some caution because of proximity in time to the autumnal equinox. However, even after the end of the equinox period, several males were still estimated to be in this region, indicating that these positions are plausible. Moreover, migrating Kirtland's warblers have been observed there, particularly along Lake Erie and Lake Ontario (Petrucha et al. 2013). After leaving this region, males flew south to an area along the coasts of North and South Carolina, stopping again before flying ~600–950 km over the Atlantic Ocean towards The Bahamas. Resting and re-fueling prior to, and just after, crossing such a large ecological barrier is important (Buler and Moore 2011). Accordingly, the coasts of North and South Carolina and the northern Bahamian islands are both likely to be important stopover sites during fall migration. Kirtland's warblers have been sighted on these islands (Haney et al. 1998), but do not winter there in significant numbers (D. N. Ewert and J. M. Wunderle pers. comm.). It is unclear why Kirtland's choose to take the seemingly riskier open ocean route, but winds may be favorable (Gauthreaux et al. 2005), making the journey over the ocean quicker and more direct.

During spring migration, individual stopover strategies varied, but we identified three stopover areas that were used by much of the population. Most males made their first stopover in Florida, shortly after making landfall. Similar to migrants crossing other ecological barriers (e.g. deserts, mountains), high-quality stopover habitat in Florida may be important for Kirtland's warblers (Buler and Moore 2011). Most males made another stopover, in northern Florida, southeastern Georgia, or southwestern South Carolina, just to the south of the Appalachians, which is presumably a formidable ecological barrier. We identified a final stopover area in Ohio and southeastern Ontario, with about a third

of the population stopping over there. Determining the exact location and habitat type of these stopover sites will be an important next step in understanding the year-round dynamics of this endangered species.

Conservation implications

Global climate change is predicted to significantly dry the Caribbean region (Neelin et al. 2006), and cause sea level rise (Nicholls and Cazenave 2010), decreasing the quality and amount of winter habitat available to Kirtland's warblers. Winter habitat for Kirtland's warblers is created through natural disturbances (e.g. fire, hurricanes), but abandoned residential, commercial, and agricultural developments, goat farms, and mowed power line corridors all also provide important winter habitat (Wunderle et al. 2010). Thus, altered fire regimes, increases in successful land developments, and region-wide decreases in agriculture all currently threaten wintering habitat (Wunderle et al. 2010, 2014). Together, the effects of climate change and anthropogenic habitat loss, will almost certainly negatively impact Kirtland's warbler performance and survival, not only during the winter (Wunderle et al. 2014), but also during spring migration and breeding (Rockwell et al. 2012). As both our tracking data and unpublished survey data (D. N. Ewert and J. M. Wunderle pers. comm.) indicate that the majority of the Kirtland's warbler population winter in the central Bahamas, future conservation efforts should focus on the central Bahamian islands.

Information is severely lacking with respect to Kirtland's warbler diet, re-fueling rates, habitat use, predation, and competition at stopover sites. Only by first identifying stopover sites can we begin to determine if the quantity or quality of stopover habitat is limiting the population. By documenting the general location of stopover sites, we have begun the process of understanding how events during stopover might shape individual performance and population dynamics. Unfortunately, our tracking data are too coarse to identify specific stopover sites and determine habitat use. However, we have significantly decreased both the spatial and temporal uncertainty regarding Kirtland's warbler stopover sites. We hope to leverage the estimated 22.5 million birders located in the states that Kirtland's warblers pass through on fall and spring migration (Carver 2011) to help us determine stopover site location and habitat use. Plans are currently underway to develop an 'eBird Kirtland's Warbler Migration Blitz', similar to the citizen science effort that has been useful in locating rusty blackbird *Euphagus carolinus* wintering sites (B. Evans pers. comm.).

The recovery of the Kirtland's warbler population from only 167 males in 1987 to over 2300 males today is a success story for the Endangered Species Act. Past conservation efforts have focused on the breeding period, but both climate change and anthropogenic habitat loss, and possibly other unknown factors, all present threats outside of the breeding period. Continued recovery and long-term sustainability will likely only be ensured by identifying limiting factors throughout the full annual cycle. By tracking Kirtland's warblers across the annual cycle for the first time, we have provided managers with a wealth of information upon which

to base decisions regarding future research and conservation priorities.

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Supplementary material (Appendix JAV-01096 at <www.avianbiology.org/appendix/jav-01096>). Appendix 1.